

# Shape Saliency Modulates Contextual Processing in the Human Lateral Occipital Complex

Christian F. Altmann, Arne Deubelius, and Zoe Kourtzi

## Abstract

■ Visual context influences our perception of target objects in natural scenes. However, little is known about the analysis of context information and its role in shape perception in the human brain. We investigated whether the human lateral occipital complex (LOC), known to be involved in the visual analysis of shapes, also processes information about the context of shapes within cluttered scenes. We employed an fMRI adaptation paradigm in which fMRI responses are lower for two identical than for two different stimuli presented consecutively. The stimuli consisted of closed target contours defined by aligned Gabor elements embedded in a background of randomly oriented Gabors. We measured fMRI adaptation in the LOC across changes in the context of the target shapes by manipulating the position and orientation of the background

elements. No adaptation was observed across context changes when the background elements were presented in the same plane as the target elements. However, adaptation was observed when the grouping of the target elements was enhanced in a bottom-up (i.e., grouping by disparity or motion) or top-down (i.e., shape priming) manner and thus the saliency of the target shape increased. These findings suggest that the LOC processes information not only about shapes, but also about their context. This processing of context information in the LOC is modulated by figure-ground segmentation and grouping processes. That is, neural populations in the LOC encode context information when relevant to the perception of target shapes, but represent salient targets independent of context changes. ■

## INTRODUCTION

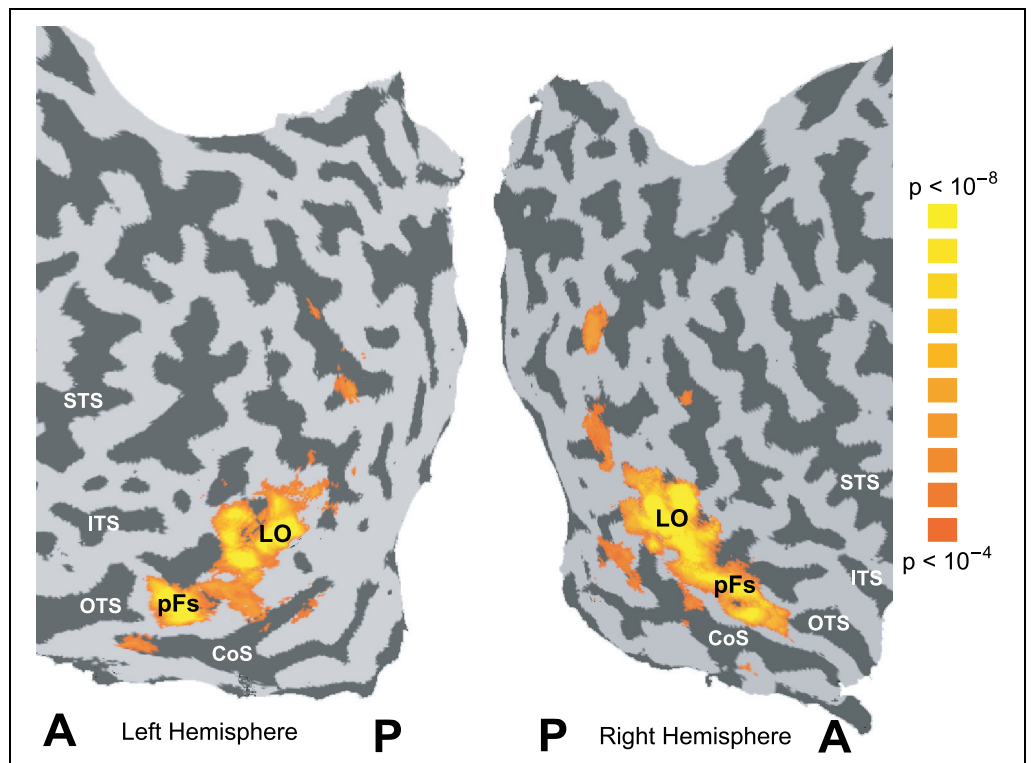
In natural environments, we encounter objects embedded in complex cluttered scenes rather than isolated from their backgrounds. Natural context influences our perception of objects. For example, the detection of a target can be impaired when it appears hidden behind occluding objects in a visual scene. One of the most important tasks of the visual system is to segment local elements from their context and integrate them into individual target objects. Many investigations from Gestalt psychology (Wertheimer, 1938; Koffka, 1935) to computational approaches (Roelfsema, Lamme, Spekreijse, & Bosch, 2002; Sigman, Cecchi, Gilbert, & Magnasco, 2001; Stringer & Rolls, 2000; Li, 1998, 1999, 2001; Stemmler, Usher, & Niebur, 1995; Grossberg & Mingolla, 1985; Grossberg, 1994) have proposed mechanisms for solving the figure-ground segmentation problem in natural scenes. Several psychophysical (Hess & Field, 1999; Field, Hayes, & Hess, 1993; Polat & Sagi, 1993, 1994; Polat, 1999; Polat & Bonnef, 2000), neurophysiological (Fitzpatrick, 2000; Lamme, Super, & Spekreijse, 1998; Lamme, & Roelfsema, 2000; Gilbert, 1992, 1998; Allman, Miezen, & McGuinness, 1985 for reviews), and imaging (Altmann, Bühlhoff, & Kourtzi, 2003; Kourtzi, To-

lias, Altmann, Augath, & Logothetis, 2003; Murray, Kersten, Olshausen, Schrater & Woods, 2002; Kastner, De Weerd, & Ungerleider, 2000) studies have investigated the mechanisms that mediate the segmentation of contour elements from their background and their integration into global shapes. However, little is known about the processing of context information, its role in shape perception and its representation in the human brain.

The present study used human fMRI to address this question. In the human brain, the lateral occipital complex (LOC), a region in the lateral occipital cortex extending anterior into the temporal cortex (Figure 1), has been implicated in the analysis of object shape (Kanwisher, Chun, McDermott, & Ledden, 1996; Malach et al., 1995) and processes of object recognition (Bar et al., 2001; Grill-Spector, Kushnir, Hendler, & Malach, 2000; Grill-Spector, Kourtzi, & Kanwisher, 2001). We asked whether neural populations in the LOC process information about the context of shapes or whether they represent shapes independent of their context.

To this end, we used closed contours that consisted of aligned Gabor elements (target shape) embedded into a field of randomly positioned and oriented Gabor elements (context) (Figure 2). Previous studies (Kovacs & Julesz, 1993; Kovacs & Julesz, 1994) have shown that these displays result in the perception of global shapes

**Figure 1.** Functional localization of the LOC. Functional activation maps for one representative subject showing the LOC. The functional activations are superimposed on flattened cortical surfaces of the left and right hemispheres. The sulci are coded in darker gray than the gyri and the anterior–posterior orientation is noted by A and P. Major sulci are labeled: STS = superior temporal sulcus; ITS = inferior temporal sulcus; OTS = occipitotemporal sulcus; CoS = collateral sulcus. The LOC was defined as the set of all contiguous voxels in the ventral occipitotemporal cortex that were significantly stronger ( $p < 10^{-4}$ ) activated by intact than by scrambled images of objects. The posterior (lateral occipital, LO) and anterior (posterior Fusiform, pFs) regions of the LOC were



identified on the functional maps based on anatomical criteria, as described previously (Grill-Spector et al., 2000). (Mean Talairach coordinates: right lateral occipital:  $37.9 \pm 1.8$ ,  $-69.4 \pm 4.3$ ,  $-8.1 \pm 3.7$ ; left lateral occipital:  $-38.1 \pm 9.1$ ,  $-72.2 \pm 7.3$ ,  $-6.7 \pm 5.0$ ; right posterior fusiform:  $31.5 \pm 3.6$ ,  $-46.8 \pm 5.0$ ,  $-15.8 \pm 2.1$ ; left posterior fusiform:  $-35.2 \pm 6.4$ ,  $-48.9 \pm 9.9$ ,  $-15.4 \pm 2.6$ ).

rather than simple paths (i.e., open contours) and entail the integration of the local target elements into salient regions (i.e., surfaces) and their segmentation from the background elements.

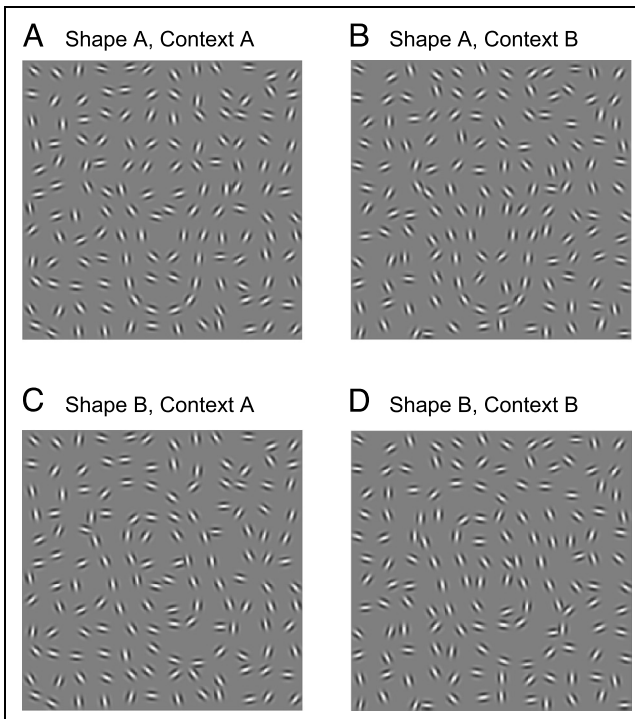
We employed an fMRI adaptation paradigm in which lower responses are observed for stimuli presented repeatedly than for different stimuli (James, Humphrey, Gati, Menon, & Goodale, 1999; Buckner, 1998; Wiggs & Martin, 1998; Miller, Li, & Desimone, 1991; Miller, Erickson, & Desimone, 1996). fMRI adaptation paradigms provide a sensitive tool that allows us to overcome the spatial resolution limitations of conventional fMRI paradigms (Avidan, Hasson, Hendler, Zohary, & Malach, 2002; Grill-Spector, Kushnir, Edelman, Avidan, Itzhak & Malach, 1999; Grill-Spector & Malach, 2001) and test whether different subpopulations of neurons in a voxel encode specific stimulus dimensions or respond invariantly across feature changes (e.g., context changes). In all experiments, two stimuli were presented sequentially in a trial with: (a) the same target shape and background (identical), (b) the same target shape, but different background (different context), (c) the same background, but different target shape (different shape), and (d) different target shape and background (completely different). Decreased responses (i.e., adaptation) in the LOC across background changes would suggest that neural populations in the LOC encode the target

shape independent of its context. However, increased responses would indicate that neural populations in the LOC encode the context of objects in a scene. We further tested the role of figure–ground segmentation in the processing of context information by manipulating the grouping of the target or background elements in a bottom-up (disparity or motion grouping) or top-down (priming of the target shape) manner. Our findings suggest that neural populations in the LOC process information not only about the target shape, but also about the context of shapes. This contextual processing in the LOC is modulated by figure–ground segmentation and grouping processes that may enhance the saliency of targets; that is, their detectability from cluttered backgrounds.

## RESULTS

### Localization of the LOC in the Human Visual Cortex

We identified the LOC as the region of interest (ROI) for each subject individually (Figure 1) and defined it as the set of all contiguous voxels in the ventral occipitotemporal cortex that were activated more strongly ( $p < 10^{-4}$ ) by intact than by scrambled images of objects, as described previously (Kourtzi & Kanwisher, 2000).



**Figure 2.** Stimuli. An example of the stimuli used in all experiments: (A) stimulus consisting of shape A embedded in context A, (B) stimulus consisting of shape A embedded in a different context B, (C) a different shape B embedded in context A, and (D) shape B embedded in context B.

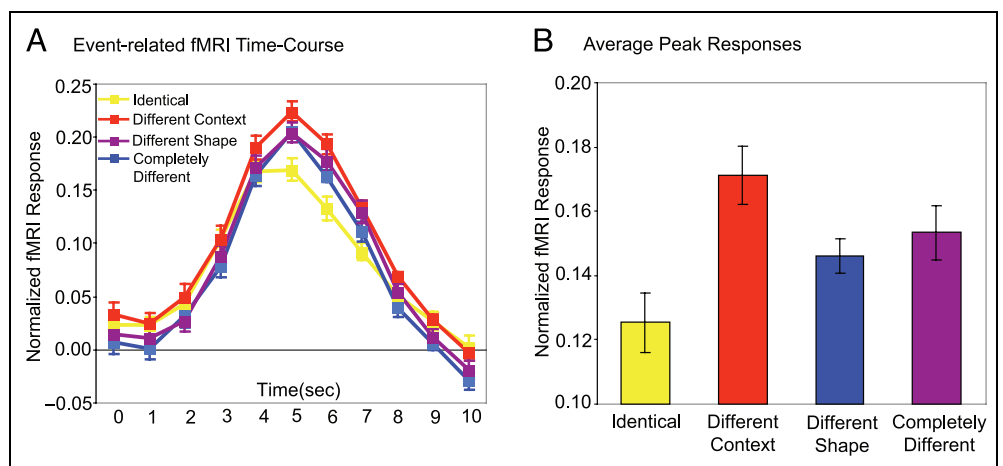
### Experiment 1: Processing of Context Information in the LOC

Experiment 1 tested for adaptation in the LOC across shape or background changes in displays of aligned

contour elements embedded in randomly oriented background elements. As shown in Figure 3, analysis of the fMRI responses in the LOC showed stronger responses when the same target was presented in a different rather than in the same context. That is, no adaptation was observed for shapes across changes in their background (different context). In particular, a two-way repeated-measures ANOVA with factors Shape (same, different) and Context (same, different) showed significantly stronger fMRI responses for different than same background [ $F(1,9) = 10.29, p < .05$ ]. These results suggest that neural populations in the LOC process information about the context of visual shapes. Surprisingly, no significant differences were observed between identical and different target shapes [ $F(1,9) < 1, p = .86$ ] in contrast to previous studies showing adaptation (i.e., decreased responses) in the LOC for the repeated presentation of the same than different shapes (e.g., Kourtzi & Kanwisher, 2000, 2001; Grill-Spector et al., 1999). These results were confirmed by contrast analysis that showed a significant difference between identical and completely different [ $F(1,9) = 4.399, p < .05$ ], but not for identical and different shape [ $F(1,9) = 2.41, p = .13$ ] conditions.

One possible explanation is that responses in the LOC depend on the amount of local information that changes across conditions. That is, the LOC responses were stronger in the different context condition where many background elements changed than in the different shape condition where only few shape elements changed. Such an explanation would contradict accumulating evidence that the LOC represents the perceived global shape rather than local features (Altmann et al., 2003; Grill-Spector et al., 2001, Kourtzi & Kanwisher,

**Figure 3.** Results for Experiment 1. fMRI responses across conditions (identical, different context, different shape, completely different) in the LOC. We plot normalized fMRI responses that were calculated individually for each subject by subtracting the mean percent signal change for all the conditions from the mean percent signal change for each condition and adding the mean percent signal change for all the conditions across subjects. (A) Event-related time courses. Time courses (percent signal change from the fixation baseline) for 11 time points.



Trials start at time 0 sec. (B) Normalized fMRI responses at the peak time points (4–6 sec after stimulus onset) show differences across conditions independent of the variability in the fMRI signal across subjects. The error bars indicate mean standard errors on the fMRI responses for each condition averaged across trials (25 per scan), scans (4), and subjects (9). Additional analysis in posterior (LO) and anterior (pFs) subregions of the LOC showed similar patterns of results in both subregions. Specifically, no interaction between target shape (same, different) and ROI (LO, pFs) was observed [ $F(1,8) < 1, p = .99$ ] and between background (same, different) and ROI (LO, pFs) [ $F(1,8) < 1, p = .77$ ]. Similar pattern of results for the LOC subregions was observed in Experiments 2 to 4.

2001). An alternative explanation is that the background elements interfere with the grouping of the shape elements and thus affect responses to global shapes in the LOC. The high similarity between the target shape and the background elements (oriented Gabors) facilitates possible interference of the background elements to the integration of the target shape. These interference effects could be enhanced in cases where the random position and orientation of the background result in spurious collinearities in the background (Figure 2). Experiments 2 to 4 addressed this hypothesis by testing whether bottom-up and top-down manipulations of the shape saliency affect the processing of shape and context information in the LOC.

### Experiments 2 and 3: Bottom-Up Modulations in the Processing of Shape Context

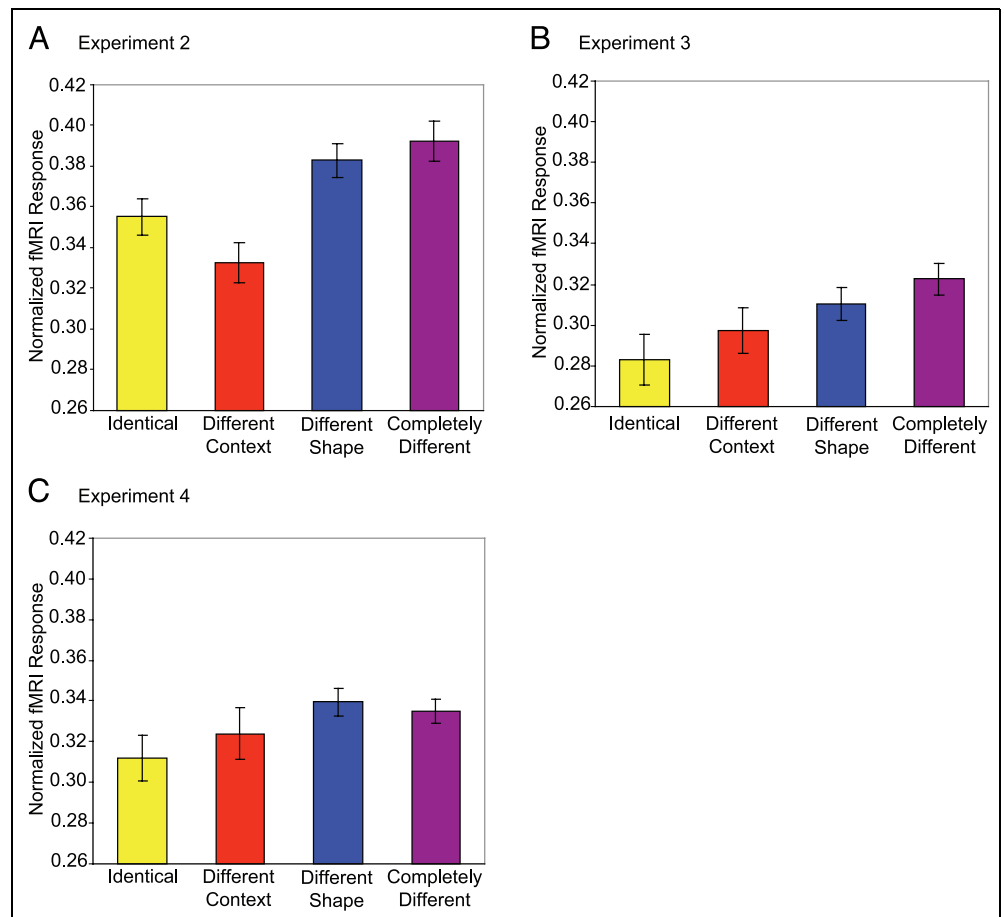
Experiments 2 and 3 tested whether the contextual effects observed in Experiment 1 were modulated when the grouping of the target elements and therefore their segmentation from the background elements was enhanced. We used the same stimuli as in Experiment 1, but presented the target shape: (a) stereoscopically in front of the background by rendering the target elements at a different disparity than the background

elements (Experiment 2) and (b) in between background elements that changed phase over time and thus appeared to be moving (Experiment 3).

In Experiment 2, as shown in Figure 4A, we observed stronger fMRI responses in the LOC for different than for identical target shapes, but no significant differences across context changes. Specifically, a two-way repeated-measures ANOVA on the fMRI responses in the LOC with factors Shape (same, different) and Context (same, different) showed significantly stronger responses for different than same target shapes [ $F(1,11) = 8.75, p < .05$ ], but no significant differences between same and different context [ $F(1,11) < 1, p = .50$ ]. A significant interaction between Shape and Context [ $F(1,11) = 6.29, p < .05$ ] was observed. Follow-up contrast analysis showed significant differences between identical and completely different [ $F(1,11) = 6.09, p = .01$ ], but not [ $F(1,11) = 2.22, p = .14$ ] between identical and different context conditions. That is, adaptation was observed for identical target shapes when embedded in the same or in a different context. These findings suggest that the facilitation of figure-ground segmentation by disparity decreases the effect of context in the integration of the target shape elements.

A possible limitation of this experiment is that the observed results could be due to more image informa-

**Figure 4.** (A) Results for Experiment 2: fMRI activations in the LOC across conditions when figure-ground segmentation was facilitated by disparity. (B) Results for Experiment 3: fMRI activations in the LOC across conditions when figure-ground segmentation was facilitated by motion of the background elements. (C) Results for Experiment 4: fMRI activations in the LOC across conditions when the target shape was primed 50 msec before the presentation of the background.



tion (disparity) on the target than on the background elements. Experiment 3 addressed this possible confound by manipulating the grouping of the background rather than the shape elements by motion due to phase changes. Thus, target saliency was enhanced by increasing the physical energy of the context rather than that of the target shape.

As shown in Figure 4B, we observed adaptation in the LOC in Experiment 3 for the same shape presented twice independent of context changes. Similarly to Experiment 2, a two-way ANOVA showed significantly stronger responses for different than same target shapes [ $F(1,12) = 8.96, p < .05$ ], but no significant differences between different and same context [ $F(1,12) = 1.64, p = .22$ ]. Similarly, contrast analysis showed significant differences between identical and completely different [ $F(1,12) = 5.93, p = .01$ ] but not [ $F(1,12) < 1, p = .38$ ] between identical and different context conditions.

In summary, the results of Experiments 2 and 3 suggest that stimulus properties (i.e., disparity and motion) that facilitate the segmentation of the target shape from the background increase the target saliency and result in processing of shapes in the LOC independent of context changes.

#### **Experiment 4: Top-Down Modulations in the Processing of Shape Context in the LOC**

Experiments 2 and 3 tested the role of shape saliency in the processing of context information in the LOC by manipulating physical properties of the target or background elements that mediated the grouping of these elements (i.e., grouping by disparity or motion). Contour integration and figure-ground segmentation have also been shown to be facilitated in a top-down manner by priming of the target shape (Beaudot, 2002; Baylis & Cale, 2001; Laarni & Nyman, 1997). In Experiment 4, we tested top-down effects in the processing of context information in the LOC by presenting the shape contours before the background elements, therefore priming the target shape and facilitating its segmentation from the context.

As shown in Figure 4C, significant differences in the fMRI responses in the LOC were observed across changes in the target shape [ $F(1,11) = 8.72, p < .05$ ], but not the context [ $F(1,11) < 1, p = .70$ ]. Further contrast analysis showed no significant differences [ $F(1,11) < 1, p = .66$ ] between identical and different context conditions. Consistent with the results of the previous experiments, these findings provide additional evidence that increased shape saliency diminishes contextual effects in the processing of shape information in the LOC.

#### **Comparison across Experiments**

The results of the presented experiments indicate that neural populations in the LOC process information about the target shapes and their context in visual scenes.

When the background elements interfere with the integration of the target elements, responses in the LOC are modulated by context changes. However, when figure-ground segmentation is facilitated and target saliency is enhanced, neural populations in the LOC appear to represent shapes independent of changes in the context.

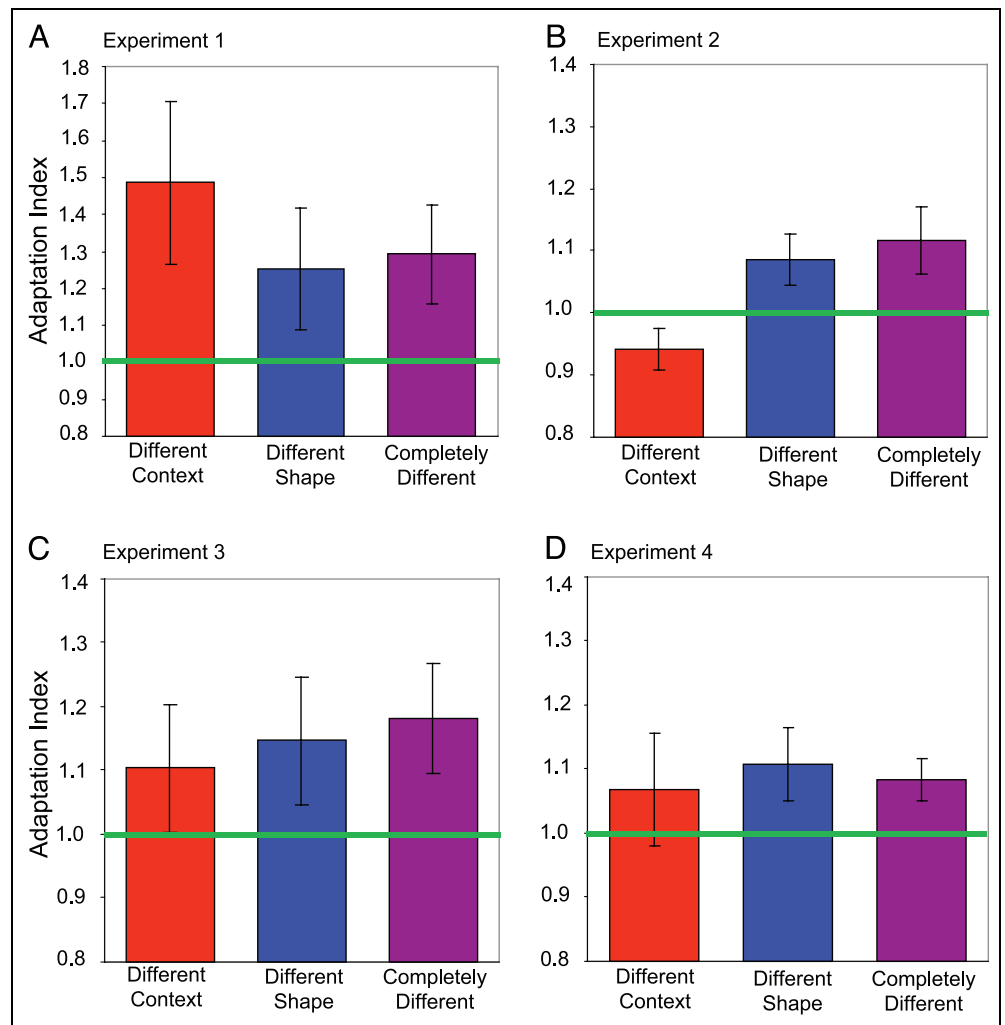
Figure 5 summarizes the fMRI adaptation effects across experiments. In particular, we plot an adaptation index that was calculated by dividing the percent signal change for each condition by the percent signal change for the identical condition for each experiment. A ratio of 1 indicates adaptation, while significantly higher responses than 1 indicate no adaptation. In Experiment 1, the adaptation index was significantly higher than 1 in the different context condition [ $t(8) = 2.20, p < .05$ ] and in the completely different condition [ $t(8) = 2.19, p < .05$ ], indicating no adaptation effect in these conditions. In all other experiments, adaptation was observed in the different context condition, suggesting that neural populations in the LOC encode the target shape independent of changes in the context when figure-ground segmentation is facilitated. In particular, in Experiment 2 the adaptation index was significantly higher than 1 in the different shape [ $t(10) = 2.11, p < .05$ ] and the completely different [ $t(10) = 2.17, p < .05$ ] conditions; in Experiment 3 in the completely different condition [ $t(12) = 2.12, p < .05$ ]; and in Experiment 4 in the different shape [ $t(11) = 1.91, p < .05$ ] and completely different [ $t(11) = 2.59, p < .05$ ] conditions.

This effect of enhanced figure-ground segmentation due to bottom-up or top-down cues observed in the fMRI data was not evident in the behavioral data, most probably because the subjects' performance on the shape matching task was at ceiling levels in all experiments. However, previous psychophysical studies provide evidence that contour integration and surface perception are facilitated by grouping cues, such as disparity (Hess & Field, 1994; Hess, Hayes, & Kingdom, 1996; Nakayama & Shimojo, 1992). Moreover, our recent fMRI studies have shown that grouping of misaligned contour elements by disparity results in increased detection performance and fMRI responses in the LOC (Altmann et al., 2003).

## **DISCUSSION**

Our findings suggest that neural populations in the LOC process information not only about visual shapes, but also their context in cluttered scenes. Specifically, shape adaptation in the LOC was modulated by shape saliency. That is, recovery from adaptation was observed when the same shape was presented at different backgrounds that consisted of similar elements as the target shape elements. However, this contextual modulation was decreased when segmentation of the target shape from the background was facilitated by grouping of the target elements in a bottom-up (feature-based grouping) or top-

**Figure 5.** fMRI adaptation index for all experiments. An fMRI adaptation index (normalized fMRI response in each condition/normalized fMRI response in the identical condition) reported for the different context, different shape, and completely different conditions for all four experiments (A–D). A ratio of 1 (green horizontal line) indicates adaptation. The error bars indicate standard errors on the normalized fMRI response averaged across scans and subjects.



down (target priming) manner. When target shapes were easy to segment from their background, the neural populations in the LOC appeared to represent shape information independent of context changes.

These findings are consistent with previous neurophysiological studies showing that the responses of inferotemporal macaque neurons to a target shape are modulated by its visual context (Missal, Vogels, & Orban, 1997; Missal, Vogels, Li, & Orban, 1999; Rolls & Tovee, 1995; Miller, Gochin, & Gross, 1993; Sato, 1989). For example, the response amplitude and the selectivity of neurons are reduced when a figure overlaps with a background shape compared to when the figure is presented in isolation (Missal et al., 1997, 1999). These suppressive effects are stronger when figure and background are less discriminable due to high physical stimulus similarities. Interestingly, these effects diminish when the target shape is fixated and thus encoded at a finer scale that may facilitate its segmentation from the background (Rolls, Aggelopoulos & Zheng, 2003; Sheinberg & Logothetis, 2001; DiCarlo & Maunsell, 2000). Thus, similar mechanisms

in the monkey and the human higher visual areas may mediate the processing of target shapes in complex visual scenes.

### Contextual Processing across Visual Areas

Taken together, our findings and previous neurophysiological studies suggest that the responses of neural populations in higher visual areas thought to be involved in visual shape analysis and object recognition (monkey IT, human LOC) are modulated by the context of visual targets. Thus, higher visual areas are involved in the segmentation of the target elements from their background and their integration into coherent global shapes.

At first glance, these findings appear to contradict accumulating evidence that contour integration (Fitzpatrick, 2000; Gilbert, 1992, 1998; Allman et al., 1985 for reviews), contour completion (Larsson et al., 1999; Sugita, 1999), figure-ground segmentation (Rossi, Desimone, & Ungerleider, 2001; Kastner et al., 2000; Lee, Mumford, Romero, & Lamme, 1998; Zipser, Lamme, &

Schiller, 1996; Lamme 1995, 1998; Lamme, & Roelfsema, 2000), and figure border assignment (Bakin, Nakayama, & Gilbert, 2000; Zhou, Friedman, & von der Heydt, 2000) are resolved at earlier stages of visual analysis (i.e., areas V1–V4). Horizontal connections in macaque V1 have been proposed to link neurons of similar orientation tuning and mediate contour integration (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Malach, Amir, Harel, & Grinvald, 1993; Gilbert & Wiesel, 1989; Gilbert, 1992, 1998).

However, our recent fMRI studies on monkeys and humans (Altmann et al., 2003; Kourtzi et al., 2003) have shown that both early and higher visual areas are involved in shape integration processes at different spatial scales. Specifically, shape integration in early visual areas appears to depend on the signal (shape elements)-to-noise (background elements) within the receptive field, while higher visual areas appear to represent salient shape regions (Stanley & Rubin, 2003) and the perceived global shape (Kourtzi & Kanwisher, 2001). Consistently, recent neurophysiological studies (Smith, Bair, & Movshon, 2002) and computational approaches (Roelfsema et al., 2002) suggest that early visual areas detect the figure–ground boundaries, but higher visual areas integrate the figure elements into a coherent representation of the figural region. Feedback from higher areas (e.g., Mareschal, Sceniak, & Shapley, 2001; Li, 2000; Lamme et al., 1998; Lamme & Roelfsema, 2000; Zipser et al., 1996; Salin & Bullier, 1995) may then modulate the visual integration processes in early visual areas. These studies suggest that feature similarity between background and figure elements may interfere with the integration of the figure and modulate the responses to shapes in higher visual areas (i.e., LOC) as observed in our experiments. When figure–ground segmentation is facilitated, the interference from the background elements is reduced and thus global shapes can be represented independent of changes in the context. Another possible explanation is that grouping or priming of the target elements results in a target pop-out effect that increases attention and thus responses to the target shape. This interpretation is consistent with previous studies showing that attention modulates shape responses in occipitotemporal areas (Avidan, Levy, Hendler, Zohary, & Malach, 2003; O’Craven, Downing, & Kanwisher, 1999; Desimone & Duncan, 1995; Braun, 1994). Further studies are required to test the role of attention in the processing of shapes in visual scenes (Driver, Davis, Russell, Turrato, & Freeman, 2001; Gilbert, Itoh, Kapadia, & Westheimer, 2000; Grossberg & Mingolla, 1985; Grossberg, 1994; Li, 1998, 1999, 2000, 2001).

## Conclusions

Our study investigated the processing of global target shapes in cluttered scenes in the human LOC, an area

known to be involved in analysis of shapes (Kanwisher et al., 1996; Malach et al., 1995) and processes of object recognition (Bar et al., 2001; Grill-Spector et al., 2000, 2001). To this end, we used stimuli with highly similar target and background elements that resemble camouflage conditions in natural images where targets are hidden due to their similarity with the background. Recent studies suggest that geometric regularities (e.g., collinearity) are characteristic of natural scenes and the primate brain has developed a network of connections that mediate contextual processing (Dragoi, Turcu, & Sur, 2001; Geisler et al., 2001; Sigman et al., 2001; Tolhurst, Tadmor, & Chao, 1992). Our study demonstrates that shape saliency modulates contextual processing in the human LOC. Specifically, neural populations in the LOC process and/or represent information about contextual elements that interfere with the integration of the target elements into a global coherent shape. When figure–ground segmentation is facilitated, neural populations in the LOC may achieve a context-invariant representation of the target shapes. Further studies are required to test whether contextual processing in displays with simpler (e.g., open contours) or more complex (e.g., familiar objects with multiple parts) stimuli than the novel closed shapes used in our study involves primarily early visual areas or regions engaged in spatial memory (Bar & Aminoff, 2003), respectively. In summary, our findings provide novel evidence for the neural basis of coherent visual perception in natural scenes and insights into the understanding of contextual effects on the spatial perception and memory of visual scenes (Chun & Jiang, 1998; Hollingworth & Henderson, 1998; Biederman, Mezzanotte, & Rabinowitz, 1982).

## METHODS

### Subjects

Forty-seven students from the University of Tübingen participated in four experiments. Ten subjects participated in Experiment 1, 12 in Experiment 2, 13 in Experiment 3, and 12 in Experiment 4. The data from one subject in Experiment 1 and from one subject in Experiment 2 were excluded due to excessive head movement.

### Stimuli

As shown in Figure 2, the stimuli used in Experiment 1 consisted of a 9.5° by 9.5° rectangular field that contained a target shape embedded in a background of randomly oriented elements. The stimuli were rendered with 144 Gabor elements, that is oriented sinusoidal luminance features (4.5 cycles per degree of visual angle) with Gaussian envelopes that model roughly the RF structure of V1 simple cells, as de-

scribed in previous studies (Altmann et al., 2003; Braun, 1999; Pennefather, Chandna, Kovacs, Polat & Norcia, 1999). The full-width at half-height of the Gabor elements was  $0.46^\circ$  and the center-to-center distance between them was on average  $1.15^\circ$ . The target shape consisted of two concentric closed contours covering an average area of  $6^\circ \times 6^\circ$ . The background consisted of randomly oriented and pseudorandomly positioned Gabor elements. Seventy different closed shapes were used in each experiment.

In Experiments 2 to 4 we used the same stimuli as in Experiment 1, but we manipulated the saliency of the target shapes by facilitating their segmentation from the background. In particular, in Experiment 2, the target shapes were presented stereoscopically in front of the background elements ( $0.23^\circ$  disparity). These stimuli were rendered as red-green anaglyphs and were presented to the observers through red-green glasses. In Experiment 3, the background elements changed phase by  $0.23^\circ$  across three frames, each one presented for 100 msec. As a result, the target shapes appeared as static in between a field of background elements moving at a speed of  $0.77^\circ/\text{sec}$ . In Experiment 4, the stimuli were presented for 350 msec, with the target shape appearing 50 msec before the background elements.

## Procedure

Each subject participated in a single session for only one of the experiments. Each experiment consisted of six scans: two LOC localizer scans and four event-related adaptation scans. The order of the scans was counterbalanced across subjects. Before the scanning session the subjects were familiarized with the stimuli during a short practice session.

For the LOC localizer scans, we used gray-scale images of novel and familiar objects as well as scrambled versions of each set, as described previously (Kourtzi & Kanwisher, 2000). Each stimulus condition was presented for four 16-sec stimulus epochs with interleaved fixation periods, in a blocked design that balanced for the order of the conditions (Kourtzi & Kanwisher, 2000). Each of 20 images for each condition was presented for 300 msec followed by a blank interval of 500 msec. The subjects were instructed to perform a one-back matching task that engaged their attention on all stimulus types (i.e., the intact and the scrambled images of objects).

In the event-related scans for each experiment, we tested four different conditions that were defined by the two stimuli presented in a trial: (a) identical context, where the same target shape in the same background was presented twice in a trial; (b) different context, where the same target shape was embedded in different backgrounds of randomly oriented Gabor elements; (c) different shape, where different target shapes were

embedded in the same background; and (d) completely different, where two different target shapes were presented in different backgrounds in a trial.

Each event-related scan consisted of one epoch of experimental trials and two 8-sec fixation epochs, one at the beginning and one at the end of the scan. Each scan consisted of 25 experimental trials for each of the 4 conditions and 25 fixation trials. A new trial began every 3 sec and consisted of a first stimulus image presented for 300 msec, an interstimulus blank of 400 msec, a second stimulus presentation for 300 msec, and a blank interval of 2000 msec. As in previous studies (Kourtzi & Kanwisher, 2000), the order of presentation was counterbalanced so that trials from each condition, including the fixation condition, were preceded (two trials back) equally often by trials from each of the other conditions. Different stimuli were presented across conditions, but all the stimuli were presented in all conditions across subjects. Subjects performed a shape matching task (same vs. different) on the two stimuli presented in a trial.

Analysis of the behavioral data showed similar results across experiments. In particular, the subject's accuracy in the shape matching task across experiments was as follows: Experiment 1 (identical: 94.3%, different context: 93.2%, different shape: 97.5%, completely different: 97.3%), Experiment 2 (identical: 94.1%, different context: 92.9%, different shape: 95.2%, completely different: 94.8%), Experiment 3 (identical: 94.3%, different context: 93.1%, different shape: 95.4%, completely different: 95.0%), Experiment 4 (identical: 97.8%, different context: 97.4%, different shape: 87.1%, completely different: 86.8%).

## Imaging

For all the experiments, scanning was done on the 1.5 T Siemens scanner at the University Clinic in Tübingen, Germany. A gradient-echo pulse sequence (TR = 2 sec, TE = 90 msec for the localizer scans; TR = 1 sec, TE = 40 msec for the event-related scans) was used. Eleven axial slices (5 mm thick with 3.00 by 3.00 mm in-plane resolution) were collected with a head coil.

## Data Analysis

fMRI data were processed using the BrainVoyager 4.9 software package. Preprocessing of all the functional data included head movement correction and removal of linear trends. The 2-D functional images were aligned to 3-D anatomical data and the complete dataset was transformed to Talairach coordinates.

For each individual subject, the LOC was defined as the ROI. 3-D statistical maps were calculated for the LOC by correlating the signal time course with a reference function for each voxel based on the hemodynamic response properties.



For each event-related scan, we extracted the fMRI response by averaging the data from all the voxels within the independently defined ROI (LOC). We then averaged the signal time course across trials in each condition at each of 11 corresponding time points (sec) and converted these time courses to percent signal change relative to the fixation trials, as described previously (Kourtzi & Kanwisher, 2000, 2001). We then averaged the time courses for each condition across scans for each subject and then across subjects. Because of the hemodynamic lag in the fMRI response, the peak in overall response and therefore the differences across conditions are expected to occur at a lag of several seconds after stimulus onset (Cohen, 1997; Dale & Buckner, 1997; Boynton, Engel, Glover, & Heeger, 1996). To find the latencies at which any effects occurred, we conducted an ANOVA on Condition (identical, different background, different shape, completely different) and Time (measurements made at latencies of 0 through 10 sec after trial onset) on the average percent signal change in the LOC for each experiment. This analysis showed significant interactions between Condition and Time [e.g., Experiment 1:  $F(30,240) = 1.67, p < .05$ ]. Contrast analysis showed significant differences between the identical and the completely different conditions for time points 4, 5, and 6 [ $F(30,240) = 13.99, p < .001$ ], indicating a basic adaptation effect, as observed in several previous studies (Kourtzi & Kanwisher, 2000, 2001; Grill-Spector et al., 1999), but not for the onset of a trial, that is, time point 0 [ $F(30,240) < 1, p = .47$ ].

The average of the response at these three time points was taken as the measure of response magnitude for each condition in subsequent analyses. The difference of the fMRI responses between the peak time points in the identical and the completely different condition in the LOC indicates the basic adaptation effect, as observed in several previous studies (Kourtzi & Kanwisher, 2000, 2001; Grill-Spector et al., 1999). Unfortunately, we were not able to obtain similar adaptation effects in early retinotopic areas possibly due to more transient adaptation responses in early than higher visual areas (e.g., Muller, Metha, Krauskopf, & Lennie, 1999).

### Eye Movement Data

Eye movements of four subjects in Experiment 1 were recorded outside the scanner. We used a video-based Eye-Link-system (SR Research, Mississauga, Ontario, Canada) and recorded eye position at a rate of 250 Hz. Saccades were detected by the EyeLink on-line parser as position changes exceeding 30°/sec. The subjects were presented with the same stimuli and performed the same matching task at a similar performance level as in the scanner. The average saccade number [ $F(3,9) < 1, p = .45$ ] and amplitude [ $F(3,9) < 1, p = .44$ ] did not differ significantly across conditions.

### Acknowledgments

We thank the group of Wolfgang Grodd at the University Clinics in Tübingen for providing the MRI facilities, and Lisa Betts, Elisabeth Huberle, Jan Jastorff, and Andrew Welchman for useful comments and discussion. This work was supported by the Max Planck Society and a McDonnell-Pew grant (3944900) to Z. Kourtzi.

Reprint requests should be sent to Zoe Kourtzi, Max Planck Institute for Biological Cybernetics, Spemannstrasse 38, 72076 Tübingen, Germany, or via e-mail: zoe.kourtzi@tuebingen.mpg.de.

The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2003-115F8.

### REFERENCES

- Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience*, *8*, 407–430.
- Altmann, C. F., Bülthoff, H. H., & Kourtzi, Z. (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Current Biology*, *13*, 342–349.
- Avidan, G., Hasson, U., Hendler, T., Zohary, E., & Malach, R. (2002). Analysis of the neuronal selectivity underlying low fMRI signals. *Current Biology*, *12*, 964–972.
- Avidan, G., Levy, I., Hendler, T., Zohary, E., & Malach, R. (2003). Spatial vs. object specific attention in high-order visual areas. *Neuroimage*, *19*, 308–318.
- Bakin, J. S., Nakayama, K., & Gilbert, C. D. (2000). Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations. *Journal of Neuroscience*, *20*, 8188–8198.
- Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context. *Neuron*, *38*, 347–358.
- Bar, M., Tootell, R. B. H., Schacter, D. L., Greve, D. N., Fischl, B., Mendola, J. D., Rosen, B. R., & Dale, A. M. (2001). Cortical mechanisms specific to explicit visual object recognition. *Neuron*, *29*, 529–535.
- Baylis, G. C., & Cale, E. M. (2001). The figure has a shape, but the ground does not: Evidence from a priming paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 633–643.
- Beaudot, W. H. (2002). Role of onset asynchrony in contour integration. *Vision Research*, *42*, 1–9.
- Biederman, I., Mezzanotte, R. J., & Rabinowitz, J. C. (1982). Scene perception: Detecting and judging objects undergoing relational violations. *Cognitive Psychology*, *14*, 143–177.
- Bosking, W. H., Zhang, Y., Schofield, B., & Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. *Journal of Neuroscience*, *17*, 2112–2127.
- Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience*, *16*, 4207–4221.
- Braun, J. (1994). Visual search among items of different salience: Removal of visual attention mimics a lesion in extrastriate area V4. *Journal of Neuroscience*, *14*, 554–567.
- Braun, J. (1999). On the detection of salient contours. *Spatial Vision*, *12*, 211–225.

- Buckner, R. L. (1998). Event-related fMRI and the hemodynamic response. *Human Brain Mapping*, *6*, 373–377.
- Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology*, *36*, 28–71.
- Cohen, M. S. (1997). Parametric analysis of fMRI data using linear systems methods. *Neuroimage*, *6*, 93–103.
- Dale, A. M., & Buckner, R. L. (1997). Selective averaging of rapidly presented individual trials using fMRI. *Human Brain Mapping*, *5*, 329–340.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- DiCarlo, J. J., & Maunsell, J. H. (2000). Form representation in monkey inferotemporal cortex is virtually unaltered by free viewing. *Nature Neuroscience*, *3*, 814–821.
- Dragoi, V., Turcu, C. M., & Sur, M. (2001). Stability of cortical responses and the statistics of natural scenes. *Neuron*, *32*, 1181–1192.
- Driver, J., Davis, G., Russell, C., Turrato, M., & Freeman, E. (2001). Segmentation, attention and phenomenal visual objects. *Cognition*, *80*, 61–95.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local “association field”. *Vision Research*, *33*, 173–93.
- Fitzpatrick, D. (2000). Seeing beyond the receptive field in primary visual cortex. *Current Opinion in Neurobiology*, *10*, 438–443.
- Geisler, W. S., Perry, J. S., Super, B. J., Gallogly, D. P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. *Vision Research*, *41*, 711–724.
- Gilbert, C. D. (1992). Horizontal integration and cortical dynamics. *Neuron*, *9*, 1–13.
- Gilbert, C. D. (1998). Adult cortical dynamics. *Physiological Reviews*, *78*, 467–485.
- Gilbert, C. D., Ito, M., Kapadia, M., & Westheimer, G. (2000). Interactions between attention, context and learning in primary visual cortex. *Vision Research*, *40*, 1217–1226.
- Gilbert, C. D., & Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *Journal of Neuroscience*, *9*, 2432–2442.
- Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research*, *41*, 1409–1422.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, *24*, 187–203.
- Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience*, *3*, 837–843.
- Grill-Spector, K., & Malach, R. (2001). fMR-adaptation: A tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293–321.
- Grossberg, S. (1994). 3-D vision and figure-ground separation by visual cortex. *Perception & Psychophysics*, *55*, 48–121.
- Grossberg, S., & Mingolla, E. (1985). Neural dynamics of perceptual grouping: Textures, boundaries, and emergent segmentations. *Perception & Psychophysics*, *38*, 141–171.
- Hess, R. F., & Field, D. J. (1994). Contour integration across depth. *Vision Research*, *35*, 1699–1711.
- Hess, R., & Field, D. (1999). Integration of contours: New insights. *Trends in Cognitive Sciences*, *3*, 480–486.
- Hess, R. F., Hayes, A., & Kingdom, F. A. A. (1996). Integrating contours within and through depth. *Vision Research*, *37*, 691–696.
- Hollingworth, A., & Henderson, J. M. (1998). Does consistent scene context facilitate object perception? *Journal of Experimental Psychology: General*, *127*, 398–415.
- James, T. W., Humphrey, G. K., Gati, J. S., Menon, R. S., & Goodale, M. A. (1999). Repetition priming and the time course of object recognition: An fMRI study. *NeuroReport*, *10*, 1019–1023.
- Kanwisher, N., Chun, M. M., McDermott, J., & Ledden, P. J. (1996). Functional imagining of human visual recognition. *Brain Research. Cognitive Brain Research*, *5*, 55–67.
- Kastner, S., De Weerd, P., & Ungerleider, L. G. (2000). Texture segregation in the human visual cortex: A functional MRI study. *Journal of Neurophysiology*, *83*, 2453–2457.
- Koffka, K. (1935). *Principles of gestalt psychology*. New York: Harcourt, Brace & Co.
- Kourtzi, Z., & Kanwisher, N. (2000). Cortical regions involved in perceiving object shape. *Journal of Neuroscience*, *20*, 3310–3318.
- Kourtzi, Z., & Kanwisher, N. (2001). Representation of perceived object shape by the human lateral occipital complex. *Science*, *293*, 1506–1509.
- Kourtzi, Z., Tolias, A. S., Altmann, C. F., Augath, M., & Logothetis, N. K. (2003). Integration of local features into global shapes: Monkey and human FMRI studies. *Neuron*, *37*, 333–346.
- Kovacs, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Sciences, U.S.A.*, *90*, 7495–7497.
- Kovacs, I., & Julesz, B. (1994). Perceptual sensitivity maps within globally defined visual shapes. *Nature*, *370*, 644–646.
- Laarni, J., & Nyman, G. (1997). Shape priming in a complex visual search task. *Vision Research*, *37*, 2561–2572.
- Lamme, V. A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *Journal of Neuroscience*, *15*, 1605–1615.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*, 571–579.
- Lamme, V. A., Super, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinion in Neurobiology*, *8*, 529–535.
- Larsson, J., Amunts, K., Gulyas, B., Malikovic, A., Zilles, K., & Roland, P. E. (1999). Neuronal correlates of real and illusory contour perception: Functional anatomy with PET. *European Journal of Neuroscience*, *11*, 4024–4036.
- Lee, T. S., Mumford, D., Romero, R., & Lamme, V. A. (1998). The role of the primary visual cortex in higher level vision. *Vision Research*, *38*, 2429–2454.
- Li, Z. (1998). A neural model of contour integration in the primary visual cortex. *Neural Computation*, *10*, 903–940.
- Li, Z. (1999). Contextual influences in V1 as a basis for pop out and asymmetry in visual search. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 10530–10535.
- Li, Z. (2000). Pre-attentive segmentation in the primary visual cortex. *Spatial Vision*, *13*, 25–50.
- Li, Z. (2001). Computational design and nonlinear dynamics of a recurrent network model of the primary visual cortex. *Neural Computation*, *13*, 1749–1780.
- Malach, R., Amir, Y., Harel, M., & Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *90*, 10469–10473.

- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *92*, 8135–8139.
- Mareschal, I., Sceniak, M. P., & Shapley, R. M. (2001). Contextual influences on orientation discrimination: Binding local and global cues. *Vision Research*, *41*, 1915–1930.
- Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience*, *16*, 5154–5167.
- Miller, E. K., Gochin, P. M., & Gross, C. G. (1993). Suppression of visual responses of neurons in inferior temporal cortex of the awake macaque by addition of a second stimulus. *Brain Research*, *616*, 25–29.
- Miller, E. K., Li, L., & Desimone, R. (1991). A neural mechanism for working and recognition memory in inferior temporal cortex. *Science*, *254*, 1377–1379.
- Missal, M., Vogels, R., Li, C. Y., & Orban, G. A. (1999). Shape interactions in macaque inferior temporal neurons. *Journal of Neurophysiology*, *82*, 131–142.
- Missal, M., Vogels, R., & Orban, G. A. (1997). Responses of macaque inferior temporal neurons to overlapping shapes. *Cerebral Cortex*, *7*, 758–767.
- Muller, J. R., Metha, A. B., Krauskopf, J., & Lennie P. (1999). Rapid adaptation in visual cortex to the structure of images. *Science*, *27*, 285, 1405–1408.
- Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 15164–15169.
- Nakayama, K., & Shimojo, S. (1992). Experiencing and perceiving visual surfaces. *Science*, *257*, 1357–1363.
- O’Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as units of attentional selection. *Nature*, *401*, 584–587.
- Pennafather, P. M., Chandna, A., Kovacs, I., Polat, U., & Norcia, A. M. (1999). Contour detection threshold: Repeatability and learning with “contour cards”. *Spatial Vision*, *12*, 257–266.
- Polat, U. (1999). Functional architecture of long-range perceptual interactions. *Spatial Vision*, *12*, 143–162.
- Polat, U., & Bonneh, Y. (2000). Collinear interactions and contour integration. *Spatial Vision*, *13*, 393–401.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research*, *33*, 993–999.
- Polat, U., & Sagi, D. (1994). The architecture of perceptual spatial interactions. *Vision Research*, *34*, 73–78.
- Roelfsema, P. R., Lamme, V. A., Spekreijse, H., & Bosch, H. (2002). Figure–ground segregation in a recurrent network architecture. *Journal of Cognitive Neuroscience*, *14*, 525–537.
- Rolls, E. T., Aggelopoulos, N. C., & Zheng, F. (2003). The receptive fields of inferior temporal cortex neurons in natural scenes. *Journal of Neuroscience*, *23*, 339–348.
- Rolls, E. T., & Tovee, M. J. (1995). The responses of single neurons in the temporal visual cortical areas of the macaque when more than one stimulus is present in the receptive field. *Experimental Brain Research*, *103*, 409–420.
- Rossi, A. F., Desimone, R., & Ungerleider, L. G. (2001). Contextual modulation in primary visual cortex of macaques. *Journal of Neuroscience*, *21*, 1698–1709.
- Salin, P. A., & Bullier, J. (1995). Corticocortical connections in the visual system: Structure and function. *Physiological Reviews*, *75*, 107–154.
- Sato, T. (1989). Interactions of visual stimuli in the receptive fields of inferior temporal neurons in awake macaques. *Experimental Brain Research*, *77*, 23–30.
- Sheinberg, D. L., & Logothetis, N. K. (2001). Noticing familiar objects in real world scenes: The role of temporal cortical neurons in natural vision. *Journal of Neuroscience*, *21*, 1340–1350.
- Sigman, M., Cecchi, G. A., Gilbert, C. D., & Magnasco, M. O. (2001). On a common circle: Natural scenes and Gestalt rules. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 1935–1940.
- Smith, M. A., Bair, W., & Movshon, J. A. (2002). Signals in macaque striate cortical neurons that support the perception of glass patterns. *Journal of Neuroscience*, *22*, 8334–8345.
- Stanley, D. A., & Rubin, N. (2003). fMRI activation in response to illusory contours and salient regions in the human lateral occipital complex. *Neuron*, *37*, 323–331.
- Stemmler, M., Usher, M., & Niebur, E. (1995). Lateral interactions in primary visual cortex: A model bridging physiology and psychophysics. *Science*, *269*, 1877–1880.
- Stringer, S. M., & Rolls, E. T. (2000). Position invariant recognition in the visual system with cluttered environments. *Neural Networks*, *13*, 305–315.
- Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature*, *401*, 269–272.
- Tolhurst, D. J., Tadmor, Y., & Chao, T. (1992). Amplitude spectra of natural images. *Ophthalmic & Physiological Optics*, *12*, 229–232.
- Wertheimer, M. (1938). Laws of organization in perceptual forms. In W. Ellis (Ed.), *A source book of gestalt psychology*. London: Routledge and Kegan Paul.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, *8*, 227–233.
- Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience*, *20*, 6594–6611.
- Zipser, K., Lamme, V. A., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience*, *16*, 7376–7389.